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PHENOLOGY OF TROPICAL TREES FROM JARI, LOWER AMAZON, II. INFLUENCE OF GENETICS AND THE ENVIRONMENT

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RESUMO — *A influência da genética na fenologia reprodutiva das árvores tropicais foi investigada através de três métodos diferentes. O primeiro envolveu a comparação da sincronia da floração e da frutificação de dez espécies de árvores de distribuição restrita, ocorrentes em oito comunidades de floresta primária localizadas no Jari, Baixo Amazonas. O segundo envolveu a comparação das médias da fenologia de frutificação de diferentes populações da mesma espécie, que diferem apenas quanto à localização. O terceiro método usou os coeficientes de correlação das variáveis pluviosidade, temperatura, floração, frutificação, copa com folhas velhas e copa com folhas novas, seguido pela regressão linear a fim de detectar a dependência de cada fase fenológica nas duas variáveis ambientais, pluviosidade e temperatura. Os resultados sugerem a existência de dois tipos de árvores. No primeiro a fenologia é controlada principalmente pelo ambiente, e, no segundo, o controle da fenologia é endógeno. Estes tipos de controle tanto podem ocorrer em todos os indivíduos de uma população quanto em apenas alguns indivíduos selecionados.*

PALAVRAS-CHAVE: Floração; Frutificação; Biologia de Populações; Sincronia.

ABSTRACT — *The influence of genetics in the reproductive phenology of tropical trees was investigated by three different methods. The first involved the comparison of the synchrony in the flowering and fruiting episodes of ten species of trees of restricted distribution, from eight primary forest communities in Jari, Lower Amazon. The second involved the comparison of the median fruiting phenologies of different populations of the same species which differed only in location. The third method used the correlation coefficients of the variables rainfall, temperature, flowering, fruiting, old canopy and entire new canopy, followed by further linear regression to detect the dependency of each phenological variable on the two environmental variables, rainfall and temperature. The results suggest the existence of two types of forest trees, one in which the phenology is controlled mainly by the environment, and another in which the control of phenology is mainly endogenous. These types of control can be either linked to all the individuals or to selected individuals of a population.*

KEY WORDS: Flowering; Fruiting; Population Biology; Synchrony.

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INTRODUCTION

Based on their primary goal, most studies of tropical forest phenology can be placed into one of two categories: (1) *Resource productivity* studies, and (2) *Biosystematic studies*. The first one, focus on how many calories a particular community produces for a particular guild. The second focus on counts of individuals of particular tree species that show a particular phenological phase.

This paper is part of a three-year phenological study carried out by the author from 1986 to 1990 in eight primary forest communities from Jari, Lower Amazon, Brazil, involving 36 monthly observations of 1508 trees of 137 tree species. Its aim was to study phenology of forest tree species, from the biosystematic perspective, that is, one in which the ecological role of a species can only be determined by the properties of its individuals (Hallam, Lassiter, Li & Suarez 1990).

In this study the character *species phenology* is equated with the compound phenology of its populations. A study of this nature requires lack of bias towards those trees which produces the most conspicuous fruits that animals eat, and a drastic minimization of gap and border effects. The first was attained simply by excluding the edibility criterion on the species selection, and the second by the random selection of the individuals to be observed. This last requires a previous inventory of the study area, and its advantage is to allow the computation of negative data. This type of phenological study answers not only when a particular species flowers or fruits, but what proportions of their individuals do so.

One of the facts of phenology already known for some time, is that the compounding of the flowering and fruiting phenologies of tropical forest communities results in clear seasonal patterns (Croat 1969; Pires-O'Brien 1993). What has not been strongly emphasized is that in a large number of tree species, the flowering and fruiting phenologies at the levels of individuals and populations do not reveal a seasonal pattern. There are two reasons why many phenology studies miss this fact. The first is failure to consider the negative data, that is data from those individuals in the population which do not flower or fruit during the course of a study. The second cause is when the study is not carried out in a closed forest situation.

A tree occurring isolated on a roadside, or in a forest gap behaves differently from another tree of the same species grown in a close forest. This is equivalent to the *group effect* reported for animals, and it simply implies the existence of both individual and community characters. Of course the community characters are influenced by different types of environmental conditions. In the tropical rain forest, light is the limiting factor. In an undisturbed primary forest, or in any old growth forest, the canopies touch one another, leaving only a small part exposed to the sun light, diminishing their photosynthetic activity and bringing the forest mosaic to the *compensation point*. When this happens, photosynthesis becomes equal to respiration and all the energy produced is spent in maintaining the plant's metabolism. All the other activities ceases, including important phenomena such as growth and reproduction.

What happens if an individual tree which has reached its *compensation point*, flowers and fruits? The likley answer is—it dies. This was observed by the author in several instances, during the course of the field study in Jari. Trees with a storm-caused trunk wound, attacked by fungi, were seen to flower, fruit and die while its nearby conspecifics remained in the vegetative stage.

The finding that only a small percentage of the individuals of a population enters the flowering stage in a particular cycle (Pires 1991, Pires-O'Brien 1993, Alencar 1990), brings the present question, to explain the mechanism that triggers an individual to enter a reproductive phase. This question is centered on the debate concerning the exogenous versus endogenous control of reproductive phenology, that is what makes a plant switch from a vegetative state to a reproductive one. Some authors attribute flowering to environmental causes, suggesting either the rainfall (Augspurger 1983) or photoperiod (Alvim & Alvim 1978). Others attribute flowering to internal mechanisms (Falcão & Lleras 1980, 1981, 1982, 1983; Falcão, Lleras & Kerr 1981 e Borchert 1983).

STUDY AREA AND METHODS

Description of the area where the study took place is given in Pires-O'Brien (1993). The eight communities studied are primary forest reserves aimed at the conservation of tree genetic resources. The area of Jari has an average precipitation of 2.115 m and average temperatures in the order of 26.4°C, as seen in Figure 1. The climate is seasonal with a mild dry season from September to November (climate formulas "B1rA'a'" in the Thornthwaite system or "Amw" in the Köppen system). The driest months contribute with only 8 % of the annual volume of rain in the region (Companhia Florestal Monte Dourado 1989).

Due to the longevity of most tropical trees it is not feasible to perform crosses of individuals showing different phenological traits and observing such traits over two or more generations, in order to study of the genetic cause of phenology. To counteract this limitation, the influence of genetics on phenology was evaluated indirectly, by measuring the synchrony between an individual and its conspecifics and the synchrony of the population. Very high synchrony implies a large influence of genetic factors. Very small synchrony implies a stronger role of the environment on the flowering and fruiting phenologies.

Ten species of trees which showed restricted site distribution were selected for this (Table 1). All the species studied, except for *Guarea kunthiana*, occurred in only one forest. Although the two populations of *Guarea kunthiana* occurred in two very close and similar forests, only one population was included in the synchrony calculation, to avoid a bias towards the environment.

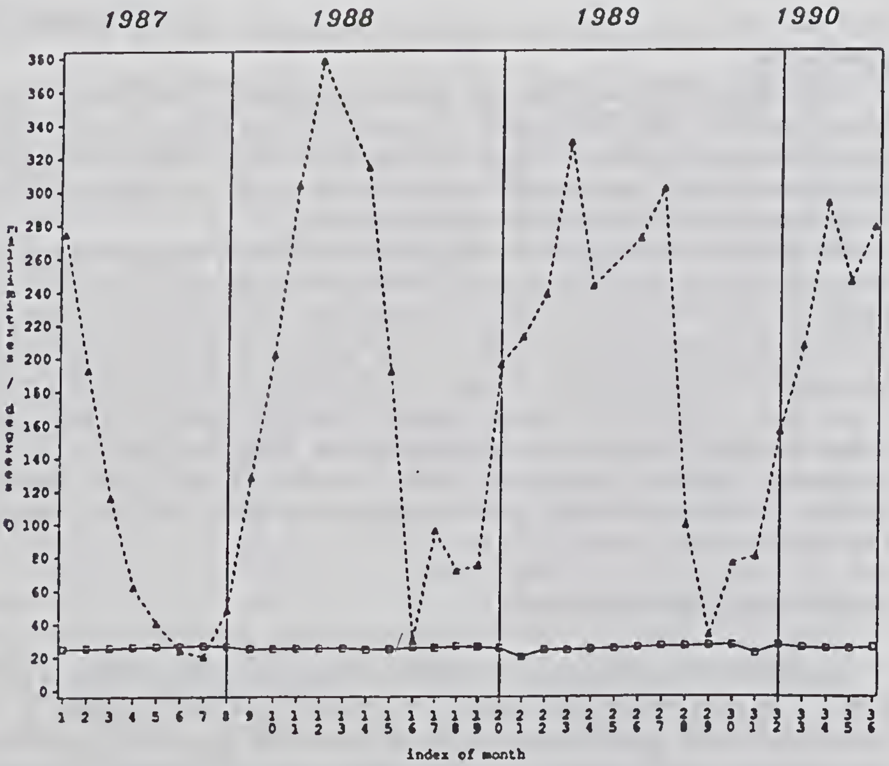

Figure 1. Rainfall and temperature during the study.

The method used to investigate synchrony among individuals of a population was that devised by Primack (1980) and modified by Augspurger (1983). This method, which was originally devised for shrubs, measures the overlap on all days an individual shrub shows at least one open flower. To adapt it to tropical trees the variable days were substituted for months and the maturity stage of the flowers was disregarded. For the synchrony calculation only those individuals that actually entered a flowering and fruiting stage were analyzed. The methods are as following:

Synchrony of a given individual with its conspecifics:

X_i, the index of synchrony for individual i, is defined as: $X_i=(1/(n-1))(1/f_i)\Sigma e_j$, where e_j = number of months both individuals i and j are flowering synchronously, and $j \neq i$; f_i = number of months individual i is flowering; n = number of individuals in the population that enter in flowering during the studied period.

Thus, when $X = 1.0$, perfect synchrony occurs, i.e., all flowering months of individual i overlap with flowering months of each other individual in the population.

When $X = 0$, no synchrony occurs, i.e., no overlap occurs among any of the flowering days of individual i and other individual j in the population.

Synchrony of the population:

Z, the index of population synchrony, is defined as: $Z = (1/n) \Sigma X_i$, where X_i is synchrony of individual i with its conspecifics from part i (above).

A second way to investigate the environmental influence on fruiting phenology was through the study of ten widely occurring species of trees, that is, species which occurred in different forest communities (Table 3). There were two reasons for choosing to compare fruiting rather than flowering. Firstly, flowering duration can be so short that it may go unnoticed in monthly observations. Secondly, the fruiting curves and peaks of individual trees resembled closely those of flowering except by being more extended (Pires 1991). Here a null hypothesis tested was that the fruiting phenologies of different populations of the same species of trees were the same. The median was used as a measure of central distribution since it permits location tests through analysis of variance of ranks. This statistical method was chosen instead of the more common ANOVA due to the skewedness of the flowering and fruiting phenologies (Pires 1991). The Kruskal-Wallis method was used for comparing the medians, since three or more statistical populations were compared. The alternative method, Wilcoxon's test is used when there only two populations to compare. A rejection of the null hypothesis implies a strong environmental control of fruiting phenology. The same can be inferred for flowering phenology since the fruiting curves are nearly the same of the flowering ones, only earlier. Fail to reject the null hypothesis supports a strong role of genetics on phenology.

For the above hypothesis, climate was assumed to be constant since all the forests studied were located within one degree of latitude/longitude, and also because no significant difference in rainfall occurred between the various climatic stations of Jari (Companhia Florestal Monte Dourado 1989). Thus soil factors and relief were the only environmental variables that could account for eventual variations in the forests studied.

A third way to investigate the influence of the environment on phenology is through the correlation coefficients of the variables *rainfall* (R), *temperature* (T), *flowering* (FL), *fruiting* (FR), *old canopy* (OC) and *entire new canopy* (E) (Tables 4 and 5). These were calculated by both the Pearson product-moment and Spearman rank methods. Finally, the data were analyzed by means of linear regression techniques in order to detect the dependency of each phenological variable (flowering/FL, fruiting/FR, old canopy/OC and entire new canopy/E) on the two environmental variables available (rainfall/R and temperature/T).

To test the null hypothesis of zero correlation, multiple regression analysis on the correlation coefficients obtained by the Spearman method was carried out in order to select which variables best explained the phenology of tropical trees, testing four phenological phases: *flowering, fruiting, old canopy* and *entire new canopy* individually as dependent variables.

RESULTS AND DISCUSSION

First the influence of genetic factors on phenology was done indirectly by comparing the synchrony of flowering and fruiting of individuals and populations. The results are given in Tables 1 (flowering synchrony) and 2 (fruiting synchrony).

Before interpreting the synchrony results, it must be pointed once again that many individual trees did not flower each year and that there were many which remained on the vegetative stage throughout the 36 months of the study. The smaller synchrony of flowering in relation to fruiting can be attributed to a larger number of variables affecting flowering including variation on the reproductive biology of each species. For instance, hermaphroditic species tend to be more asynchronous than dioecious species since asynchrony could reduce geitonogamy and promote out-crossing by forcing pollinators to move between plants (Rathcke & Lacey 1985). By the same token, monoecious plants tend to be less synchronous than dioecious since within an individual plant the female phase may be separated from the male phase by a month or longer, to promote out-crossing (Rathcke & Lacey 1985). For these reasons there seems to be advantages in the variation of flowering phenology within individuals of the same species.

In Table 3, below, fruiting phenology is studied by comparing populations of ten widely occurring tree species.

In Table 3 six species of trees had the null hypothesis of equal phenology rejected (#), meaning that they had different fruiting phenology between sites. This suggests that for such species the control of phenology is mostly exogenous (environmental). The four species which the null hypothesis of equal phenology was not rejected, *Hirtella bicornis*, *Eschweilera coriacea*, *Carapa guianensis*, and *Piptadenia communis*, the control of phenology is likely to be genetic.

The third way to look at the influence of the environment, was the correlation of *rainfall* (R) and *temperature* (T) with phenology. This approach did not address the biological species but the overall area where the phenology study took place. The phenology phases chosen to study the correlation with rainfall and temperature were: *flowering (FL)*, *fruiting* (FR), *old canopy* (OC) and *entire new canopy* (E). This was done in two steps. First, the Spearman rank correlation coefficients and the Pearson product-moment correlation coefficients on environmental and phenological variables, were calculated. Secondly, the probability for a null hypothesis of zero correlation was calculated (Table 4).

Table 1. Index of flowering synchrony of individuals and populations of ten tropical tree species.

Family / Species	**Individual**	**Population**
ANACARDIACEAE		
Tapirira sp. nov.	0,0.25,0,0	0.06
T. peckoltiana	0.66,0.66,0.16,0.5	0.39
Thyrsodium guianense	0.65,0.79,0.65,0.56,0.62,0.73,0, 0.47,0.49,0.45,0,0.37,0.57,0.35	0.48
T. spruceanum	0.5,0,0.5,0.5,0.5	0.40
LECYTHIDACEAE		
Lecythis corrugata	(none flowered)	
L. lurida	0.71,0.14,0,0.14,0.07,0.36, 0.38,0.71	0.31
MELIACEAE		
Guarea kunthiana	0.06,0.10,0,0.40,0.12,0.40	0.18
G. macrophylla	(none flowered)	
VOCHYSIACEAE		
Qualea coerulea	(none flowered)	
Q. albiflora	0.41,0.50,0.33,0.33,0,0.16, 0,0.33	0.30

Table 2. Index of fruiting synchrony of individuals and populations of ten tropical tree species.

Family / Species	**Individual**	**Population**
ANACARDIACEAE		
Tapirira sp. nov.	0,0.08,0,0.1	0.22
T. peckoltiana	0.8,0,0,0,0.57	0.27
Thyrsodium guianense	0,0.4,0.42,0.5,0.5,0.42,0,0.35, 0.3,0.4,0,0.25,0.20,0.45	0.31
T. spruceanum	0.1,0.5,1,0	0.50
LECYTHIDACEAE		
Lecythis corrugata	0,0,0,0	0
L. lurida	0.69,0.69,0.69,0.08,0.69,0.75, 0.69,0.75,0	0.56
MELIACEAE		
Guarea kunthiana	0.13,0.33,0.06,0.16	0.17
G. macrophylla	0.75,1,0,0.21	0.65
VOCHYSIACEAE		
Qualea coerulea	(none fruited)	
Q. albiflora	0,0,0	0

Table 3. Comparison of the fruiting phenology between populations of ten tree species.

Family	Species	X^2	df	$p>X^2$
Buseraceae	*Protium sagotianum*	13.43	4	0.0093#
Chrysobalanaceae	*Hirtella bicornis*	5.95	5	0.3114
Lecythidaceae	*Eschweilera coriacea*	1.60	2	0.4500
Meliaceae	*Carapa guianensis*	3.36	3	0.2861
Leguminosae	*Dinizia excelsa*	26.96	3	0.0001#
Leguminosae	*Marmaroxylon racemosum*	20.40	6	0.0011#
Leguminosae	*Pseudopiptadenia psilostachya*	2.97	4	0.5632
Myristicaceae	*Iryanthera sagotiana*	12.45	4	0.0143#
Myristicaceae	*Virola michelii*	58.40	5	0.0001#
Vochysiaceae	*Qualea paraensis*	10.92	3	0.0122#

X^2 = test statistic; df = degrees of freedom = nº of populations - 1; p = probability of observed test statistic.

Less correlation was found through the Pearson method than through the Spearman method. For this reason only the later is shown in this paper (Table 4). Here the variable *old canopy* correlated with *entire new canopy*, *flowering*, *rainfall and temperature*. The variable *entire new canopy* correlated with *old canopy*, *flowering* and *rainfall*. *Flowering* correlated with *entire new canopy rainfall* and *temperature*. *Fruiting* correlated only with *rainfall*. The variable *rainfall* correlated with *old canopy*, *entire new canopy*, *flowering* and *temperature*. *Temperature* correlated with *old canopy*, *flowering* and *rainfall*.

Studies on flowering and fruiting phenologies of 82 trees of *Copaifera multijuga* occurring in Reserva Ducke, near Manaus, also showed a strong correlation of these events with the area's seasonality (Alencar 1988).

The results of multiple regression analysis on the correlation coefficients obtained are given in Tables 5, 6 and 7, below.

Regression analysis in Tables 5, 6 and 7 showed that the four phenological phases tested: old canopy, entire new canopy, flowering and fruiting, correlated with rainfall, but not with temperature. Some correlations were also found amongst the phenological phases themselves. However, these correlations were at a micro-region level and do not constitute proof that the same correlation would occur at individual and population level.

Further interpretations of phenology at individual and population level are being prepared by the author (firstly: Pires-O'Brien et al., 1994). These papers aim to discuss phenology of each species within the light of its natural history.

Table 4. Spearman rank correlation coefficients on environmental and phenological variables, together with the calculated probability for a null hypothesis of zero correlation.

	OC	E	FL	FR	R	T
OC	1.00 0.00					
E	-0.88 0.00	1.00 0.00				
FL	-0.59 0.00	0.51 0.00	1.00 0.00			
FR	-0.04 0.81	0.15 0.37	0.23 0.18	1.00 0.00		
R	0.55 0.00	-0.48 0.00	-0.69 0.00	0.30 0.08	1.00 0.00	
T	-0.47 0.00	0.30 0.08	0.55 0.00	-0.18 0.30	-0.60 0.00	1.00 0.00

OC = old canopy; E = entire new canopy; FL = flowering; FR = fruiting; R = rainfall; T = temperature

CONCLUSION

The evidence based on the results of flowering and fruiting synchrony is that the two types of control, endogenous and exogenous, may occur within the same species, manifesting differently among the individuals of a population. This plus the comparative results of populations in different locations suggest the existence of two types of forest trees. In the first type, phenology is mainly controlled by the environment, and in the second type, the control of phenology is mainly endogenous. The two types of control can be extensive to all or may affect only some the individuals of a biological species. In this study the tree species whose phenology seemed to have a stronger genetic control were mainly *r* type opportunists, *except for Carapa guianensis* which seems to have an intermediate position in the r-K selection gradient.

The present paper compels a revisit of two major insights with respect of a species biology. The first one relates to the role of an individual with respect to its

Table 5. Mean square error for model of *flowering* (fl) as dependent variable.

Variables	Ind. Variables	R-square	Mean Square Error
1	rainfall	0.33	19.86
2	rainfall, fr	0.51	15.12
3	rainfall, fr, e	0.52	15.33
4	rainfall, fr, e, oc	0.57	13.97
5	rainfall, fr, e, oc, temp	0.57	14.37

Table 6. Mean square error for model of *fruiting* (fr) as dependent variable.

Variables	Individual variables	R-square	Mean Square Error
1	fl	0.07	33.77
2	fl, rainfall	0.30	26.17
3	fl, rainfall, e	0.38	23.96
4	fl, rainfall, e, oc	0.40	24.06
5	fl, rainfall, e, oc, temp	0.40	24.77

Table 7. Mean square error for model of *old canopy* (oc) as dependent variable.

Variables	Ind. Variables	R-square	Mean Square Error
1	rainfall	0.28	506.92
2	rainfall, fr	0.34	479.34
3	rainfall, fr, fl	0.34	492.53
4	rainfall, fr, fl, temp	0.34	507.80

species and of the species upon the community. The second insight is a philosophical one and has to do with the meaning the word *cause*, since the aim of this paper was to determine the cause of flowering phenology, that is, whether it was the environment or the plant's genetic make up.

There are two types of causes, the proximal and the ultimate cause. Proximal cause is equivalent to the physiological event closest to the one we are trying to explain. Ultimate cause refers to an evolutionary adaptation, or the sum hereof, which resulted on a particular trait. The proximal and ultimate causes are linked by the requirements and pressures of the environment, to which the species have two ways of responding: (i) by evolving through natural selection and (ii) by triggering some aspect of their anatomical or physiological machinery. As pointed by Wilson (1975), in ecological studies involving species of long life cycle the two processes seem decoupled due to the fact that the organisms are observed from the perspective of one life cycle only.

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